Why Do Animals Have So Many Receptors? The Role of Multiple Chemosensors in Animal Perception

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Abstract. Many animals have an abundance and diverse assortment of peripheral sensors, both across and within sensory modalities. Multiple sensors offer many functional advantages to an animal's ability to perceive and respond to environmental signals. Advantages include extending the ability to detect and determine the spatial distribution of stimuli, improving the range and accuracy of discrimination among stimuli of different types and intensities, increasing behavioral sensitivity to stimuli, ensuring continued sensory capabilities when the probability of damage or other loss of function to some sensors is high, maintaining sensory function over the entire sensory surface during development and growth, and increasing the richness of behavioral output to sensory stimulation. In this paper, we use the crustacean chemosensory system as the primary example to discuss these functions of multiple sensors. These principles may be applicable to the function of autonomous robots and should be considered in their design.

Introduction

Each animal has a plethora of peripheral sensors that enable the detection of different sensory stimuli, including light, chemicals, vibrations, and many others. The number of sensors that an animal possesses can be exceedingly high. In many animals, the complement of receptor cells far exceeds the number of central neurons that process sensory information. This is particularly true for the chemical senses. For example, decapod crustaceans have millions of chemosensory neurons in their cephalic and thoracic appendages (Derby and Atema, 1988; Laverack, 1988a, b; Derby, 1989; Cate and Derby, 2000), and mammals have tens of millions of olfactory receptor neurons (Hildebrand and Shepherd, 1997; Weiler and Farbman, 1997). Convergence ratios between peripheral and central olfactory neurons can be as high at 300:1 in invertebrates and vertebrates (Meisami, 1989; Ache, 1991; Schmidt and Ache, 1996b; Hildebrand and Shepherd, 1997). Within a sensory modality, an animal also typically has a diversity of sensor types.

What factors explain why animals have multiple sensors? One answer to this question is a general one: each animal has a rich diversity of behaviors that enable the acquisition of resources needed to survive and reproduce, and extensive sensory information is required to perform these behaviors. Thus, sensory systems have evolved to extract information about the quality and quantity of important environmental stimuli, such as the variety of wavelengths, intensities, and patterns that constitute each animal's sensory world.

In this paper, we offer explanations for the multiplicity of peripheral sensors. We argue that multiple sensors function in one or more of the following ways: (1) extend the range of spatial sampling by increasing the sensory surface area; (2) extend the range of types of stimuli that are discriminated by having a diversity of sensors, each of which is tuned to a subset of stimulus qualities, intensities, or temporal dynamics; (3) increase the sensitivity and accuracy of resolution through response summation; (4) maintain the function of the system in the face of damage to sensors; (5) compensate for non-functioning developmental stages of sensors; (6) enable formation of specialized central processing centers with different behavioral functions.

In developing the ideas in this paper, we draw heavily from the chemical senses of crustaceans, although some examples from other animals and sensory systems are included. Nonetheless, the principles are general. Additionally, we argue that these principles of multiple sensors may be applicable to autonomous robots and should be considered in their development.

Multiple Sensors Enhance the Probability of Detecting Stimuli by Enlarging the Sensory Surface Area

Having sensors distributed across an animal's entire body surface increases the chances that the animal will encounter environmental chemical signals. In fact, chemoreceptors are distributed across the body surface of many animals, including vertebrates (fish: Caprio, 1988) and invertebrates (insects: Dethier, 1976). In crustaceans, receptor neurons are packaged into cuticular extensions of the exoskeleton, called sensilla. Chemosensilla of crustaceans are present on most or all surfaces (Laverack, 1988a; Derby, 1989; Cate and Derby, 2000), enhancing the probability that chemical signals will be encountered.

A Diversity of Sensor Types Enhances the Ability to Discriminate Stimulus Attributes

Although chemosensors are found all over the body and appendages of crustaceans, there exists a diversity of chemosensors with a variety of properties. Having an extensive variety of sensors that extract different stimulus features should allow an animal to have a more accurate representation of its environment and aid in the discrimination of these stimuli. The sensors covering the body surface of an animal differ in structure, innervation, and distribution, reflecting different functions. In the case of insect chemosensilla, the diversity is immense: gustatory sensilla and olfactory sensilla differ in some fundamental features, but much of the diversity is within either the olfactory or gustatory modality (Dethier, 1976; Altner *et al.*, 1981; Shanbhag *et al.*, 1999). The diverse types of crustacean chemosensilla include unimodal sensilla—*e.g.*, aesthetasc sensilla (Grünert and Ache, 1988; Hallberg *et al.*, 1997), and bimodal (chemo-mechano) sensilla—*e.g.*, hair pegs, hedgehog and fringed sensilla, hooded sensilla, simple sensilla (Altner *et al.*, 1983; Schmidt and Gnatzy, 1984; Derby, 1989; Schmidt, 1989; Cate and Derby, 2000). The sensilla can be short (*e.g.*, hair pegs and hooded sensilla are *ca.* 50 μm) or long (aesthetascs can be >600 μm and guard setae can be >1200 μm) (Cate and Derby, 2000). These different sensillar types often have restricted distributions. For example, aesthetascs are only on the distal half of antennular lateral flagella, and hedgehog and fringed sensilla are only on the distal two segments of some legs.

The specific distributions, structure, and innervation of different sensilla undoubtedly have functional conse-

quences. For example, the location of aesthetascs at the anterior end of the animal places them where odor-laden currents often first reach an animal and also where fan organs can direct odors toward or away from their own sensors (Breithaupt, 2001). In the same way, chemoreceptors on the tips of legs are more likely to encounter chemicals associated with the objects in the substrate, and chemoreceptors around the mouth will receive maximal stimulation when food is held in the mouthparts.

The fact that some sensilla are innervated by both chemoreceptor neurons and mechanoreceptor neurons makes these bimodal sensilla ideal for identifying the spatial location of chemotactile stimuli, especially if the axons of these neurons project topotopically into the central nervous system. There is evidence that mechanoreceptor neurons and chemoreceptor neurons from bimodal sensilla on the antennules project to the same central neuropils (Schmidt *et al.*, 1992; Schmidt and Ache, 1996a), but it is not known if their maps are overlapping as in some insects (Newland *et al.*, 2000), or what is the spatial relationship between projections from mechanoreceptor neurons and chemoreceptor neurons from the same sensillum.

A sensory appendage can have a variety of chemoreceptor neurons that differ in their sensitivities. Antennular chemoreceptor neurons of lobsters have diverse sensitivities to different types or qualities of odorants, thus broadening the range of chemical signals to which the entire organ is sensitive (Derby and Atema, 1988; Voigt and Atema, 1992; Derby, 2000). Antennular chemoreceptor neurons also differ from each other in their sensitivities to odor concentrations (Derby and Atema, 1988; Merrill *et al.*, 1994; Daniel *et al.*, 1996) and in their ability to follow high-frequency odor pulses (*e.g.*, flicker-fusion properties) (Gomez *et al.*, 1999). Thus, different neurons extract different stimulus features, together building an image of the chemical and mechanical features of the external world.

Multiple Sensors Increase Response Sensitivity Through Response Summation

Having multiple sensors allows animals to detect lower amplitude signals. This is because central neurons can sum responses from many sensory neurons, increasing signal capturing and the signal-to-noise ratio and thus allowing finer resolution between related signals (Van Drongelen *et al.*, 1978; Meisami, 1989). For example, olfactory systems typically have at least tens to hundreds of thousands of receptor cells (Chase, 1986; Ache, 1991; Farbman, 1992; Hildebrand and Shepherd, 1997). If each neuron responded to one chemical with one spike above spontaneous activity and to another chemical with two spikes, a summation involving all neurons would dramatically amplify the difference in the magnitude of the responses to the two stimuli,

thus providing the multineuronal system with a resolving capacity far beyond that of one or a few neurons.

Multiple Sensors Ensure Functional Integrity of a Sense Organ Following Localized Damage

Multiple sensors may serve to compensate for local damage to sensory organs. Given that chemosensors are used to probe an animal's external environment for chemical signals, these sensors are often highly exposed and vulnerable to physical, chemical, and biological damage. Damage can affect sensory function (Hamilton and Case, 1983; Bauer, 1989), but multiple sensors minimize the impact of damage by increasing the probability that some sensors are undamaged and functional (Daniel et al., 2000). As an example, aesthetascs are repeating functional units, each containing a broad complement of receptor neurons with different sensitivities (Spencer, 1986; Mellon and Alones, 1993; Steullet et al., 2000b). This type of organization ensures that localized damage does not have significant impact on an animal's ability to respond to and discriminate different types of chemicals (Steullet et al., 1999, 2000c; Horner et al., 2000). In addition, many chemoreceptor systems, including the aesthetasc system, have mechanisms for self-renewal. Continuous turnover, including addition and loss, of chemoreceptors occurs in the vertebrates (Weiler and Farbman, 1997; Calof et al., 1998) and invertebrates (Chase, 1986; Chase and Rieling, 1986; Sandeman and Sandeman, 1996; Steullet et al., 2000a; Harrison et al., 2001a, b). This turnover enables the renewal of neurons that have a finite life span, which helps to maintain function of a system over time in spite of damage. Similar turnover also occurs in crustacean mechanoreceptor sensilla (Macmillan et al., 1998; Steullet et al., 2000a).

Multiple Sensors Compensate for Nonfunctioning Developmental Stages of Sensors

As animals develop and grow, they must add new sensors to maintain sensitivity over their enlarging body surfaces. To ensure that the animals can detect chemicals that impinge anywhere on the body surface, the number of sensors must increase both during development (Schafer and Sanchez, 1973; Laverack, 1988b) and throughout the lives of those species with indeterminate growth (Mellon and Alones, 1993). The antennular receptors of crustaceans are added as units in two ways (Sandeman and Sandeman, 1996; Steullet et al., 2000a). First, the antennule is composed of many segments called annuli, and new annuli are added at molting. Second, new sensilla are added to existing annuli. In some cases, such as aesthetascs and their associated chemo-mechanoreceptive sensilla, new sensilla are added in highly organized spatial arrays. In this way, the addition of annuli and sensilla creates a multiplicity of repeating, modular packages of sensors.

In addition, turnover of neurons in olfactory systems causes some neurons to be nonfunctional because they are either immature or senescing (Chase, 1986; Farbman, 1992; Steullet et al., 2000a). Since the percentage of nonfunctional cells is high in the vertebrates and invertebrates, there could be compensation by maintaining large numbers of sensors (Chase, 1986).

Multiple Sensors Enable Formation of Specialized Central Processing Centers With Different Behavioral Functions

If different sensor types are differentially coupled to central processors and motor programs, then a greater richness in behavioral outputs should be possible. For example, it has been demonstrated that the function of a chemosensory neuron in Caenorhabditis elegans is determined by that neuron's central connections rather than by the receptor molecules that it expresses (Troemel et al., 1997). Crustaceans have not only a diversity of antennular chemo- and mechanoreceptor types but also a diversity of sensory neuropils that receive their projections. These sensory neuropils include olfactory lobes (OLs), which receive input from aesthetasc chemoreceptors (Mellon and Munger, 1990; Sandeman et al., 1992; Schmidt and Ache, 1996b); lateral antennular neuropils (LANs), which are thought to receive input from non-aesthetasc chemoreceptors and mechanoreceptors on both lateral and medial antennular flagella (Schmidt et al., 1992; Schmidt and Ache, 1996a; Roye et al., 2000); and median antennular neuropils (MANs), which receive projections from statocysts, equilibrium receptors, and receptors from the antennular proximal segments (Sandeman et al., 1992; Schmidt et al., 1992; Schmidt and Ache, 1993, 1996a; Cate and Roye, 1997). The organization of these neuropils gives hints about their function. The OLs have a glomerular neuropil, similar to the olfactory neuropils of insects (antennal neuropils) and vertebrates (olfactory bulbs), in which the glomeruli represent different but overlapping chemical sensitivities (Hildebrand and Shepherd, 1997). This suggests that OLs encode chemical quality and are involved in olfactory discrimination. The LANs have a bilobed organization, with each lobe receiving input from one of the two antennular flagella (Schmidt et al., 1992). Additionally, the lobes have a stratified organization, reflecting regionalized sensory input and stratified motor output from antennular motor neurons (Schmidt et al., 1992; Schmidt and Ache, 1996a). This organization suggests that LANs may function in the sensori-motor control of antennular behavior, including flicking (Maynard, 1966) or discriminating the location of chemo-mechanostimulation on the antennule. The MANs are involved in maintaining equilibrium (Sandeman et al., 1992; Schmidt and Ache, 1993; Cate and Roye, 1997), but their function may be broader than this (Fraser, 2001).

Our analyses of the function of the different types of antennular sensors and antennular sensory neuropils in Caribbean spiny lobsters suggest that there is some overlap in chemosensory function of the aesthetasc/OL pathway and the non-aesthetasc/LAN pathway (Steullet *et al.*, 1999, 2000c; Horner *et al.*, 2000). Our working hypothesis is that antennular chemosensory neuropils have both unique and overlapping functions. Overlapping functions may include resolution of temporal characteristics of odors and mediation of discrimination of odors such as food-related chemicals. Functions unique to a neuropil may include, for the OLs, processing of pheromones (Gleeson, 1991), and for the LANs, determining location of chemotactile antennular stimulation and thus controlling local antennular reflexes (Maynard, 1966; Schmidt *et al.*, 1992; Schmidt and Ache, 1993, 1996a; Roye *et al.*, 2000).

Multiple Sensors and the Design of Autonomous Robots

Based on the assumption that the design of animals provides a guide for the principles to be used in constructing autonomous robots, we argue that such robots should have multiple sensors with the following characteristics. The sensors are sufficiently spatially distributed to sample stimulus space. They are sufficiently redundant to allow for signal summation and the resultant enhancement in sensitivity and resolving power. They are sufficiently diverse to sample the different stimulus qualities, intensities, and temporal profiles. Self-repair of sensors in autonomous robots may be too complicated to be feasible, but the functional equivalent could be achieved by having redundant sensors, only some of which are physically or functionally operational at any one time. Dysfunction of some sensors could be detected and automatically compensated by bringing back-up sensors of similar types on-line. Such a system could function as a self-repair mechanism while limiting the energy demands and processing requirements of having all sensors simultaneously and constantly functional. Sensors with different sensitivities should be connected to the integrative and motor systems related to their function, such as attraction or avoidance.

Acknowledgments

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